

A new etching trace from the Savignone Conglomerate (Oligocene), NW Italy, probably produced by limpet gastropods

ALFRED UCHMAN¹ and BRUNO RATTAZZI²

¹ Institute of Geological Sciences, Jagiellonian University, Gronostajowa 3a, PL-30-387 Kraków, Poland.

E-mail: alfred.uchman@uj.edu.pl

² Museo Paleontologico di Crocefieschi, Via alla Chiesa 12, 16010 Crocefieschi (Genova), Italy.

ABSTRACT:

Uchman, A. and Rattazzi, B. 2018. A new etching trace from the Savignone Conglomerate (Oligocene), NW Italy, probably produced by limpet gastropods. *Acta Geologica Polonica*, **68** (4), 651–662. Warszawa.

A new ichnogenus and ichnospecies (*Solealites ovalis*) of etching trace is preserved on the surfaces of clasts from the Savignone Conglomerate (Oligocene) in the Palaeogene Piemonte Basin in NW Italy. It is a shallow, oval depression with a central elevation, which was produced probably by limpet gastropods and served as their home scar, but other gastropods or even sea anemones are not excluded as the trace makers. The conglomerate is interpreted as a deposit of a fan delta, whose clasts have been bioeroded in an intertidal and shallow subtidal shore zone and redeposited to the deeper sea.

Key words: Bioerosion; Ichnotaxonomy; Fan delta; Borings; Attachment; Limpet gastropods.

INTRODUCTION

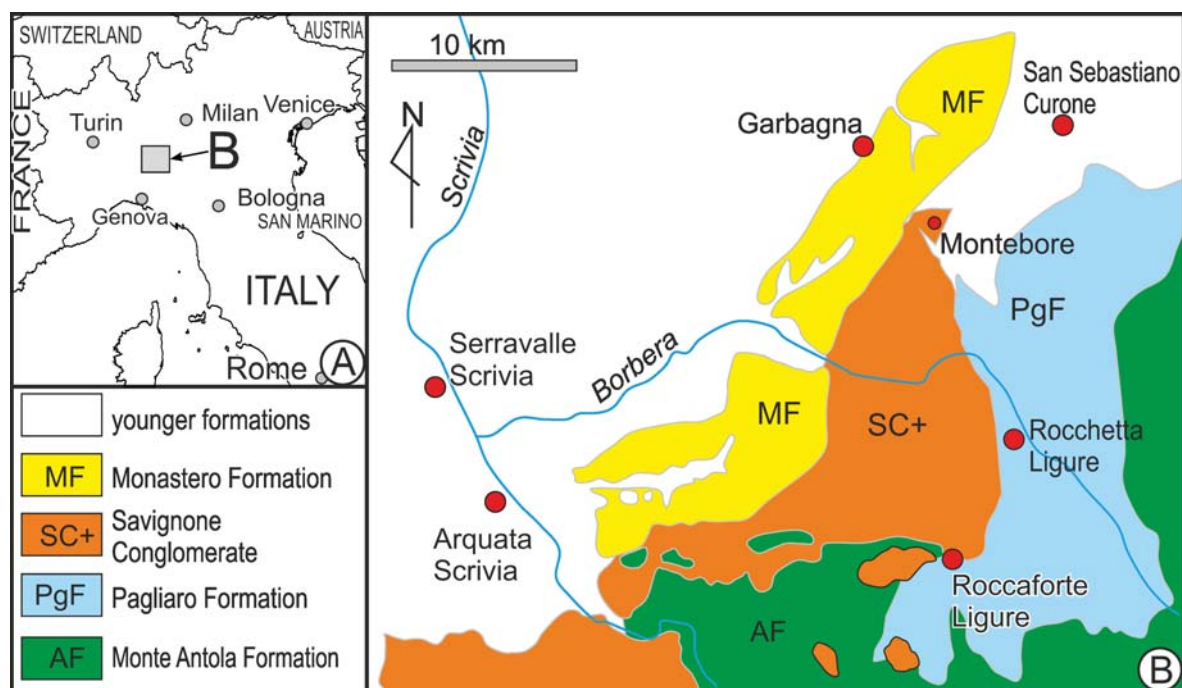
Several benthic organisms attach themselves to hard substrates on the sea floor in order to stabilise their body position and to protect against waves and predators. Some of them etch the substrate and leave characteristic traces of repeatable morphology (category fixichnia; see Gibert *et al.* 2004), which are called attachment scars or traces (e.g., Radwański 1977) and have ichnotaxonomic names (e.g., Bromley and Heinberg 2006; Neumann *et al.* 2015 and references therein). Their list is not closed and several new ichnotaxa have been added in the latest two decades, including *Spirolites radwanskii* igen. nov., isp. nov. from the Miocene of central Poland (Uchman *et al.* 2018).

In this paper, a new taxon of etching trace is presented and interpreted. It was found on a few pebbles in one locality in the Savignone Conglomerate (Oligocene), NW Italy. Several ichnotaxa of borings produced mainly by bivalves and polychaetes

have been already described from the conglomerate (Uchman *et al.* 2017a) but the trace fossil presented was not so far encountered there or anywhere else.

GEOLOGICAL SETTING AND LOCALITY

The Savignone Conglomerate (lower Oligocene: lower–middle Rupelian) is the basal unit of the Palaeogene part of the Piemonte Basin in the Borbera Valley region in the Ligurian Apennines. It forms a huge, lens-shaped lithosome resting discordantly on deep-sea flysch sediments of the Monte Antola (Campanian–Paleocene), the Pagliaro (Paleocene) and the “Ranzano” (upper Eocene) formations, which belong to the Ligurian units in the Northern Apennines. The Savignone Conglomerate is 1300 m thick (Gnaccolini 1974, 1988) but other authors estimate it at 1500 m (Ibbeken 1970), 2200 m (Van der Heide 1941; Marroni *et al.* in press), or even 2500 m (Gelati and Gnaccolini



Text-fig. 1. Location maps. A – Map of northern Italy and surroundings with indication of the study region shown in B. B – Simplified map showing the major formations in the study area (based on the Geological Map of Italy, scale 1: 100,000, sheets: Genova, Alessandria, Voghera, Rapallo – Anonymous 1969a, b, c, 1971; and at the scale 1:50,000, sheet Cabella Ligure – Marroni in press) showing the Montebore locality

1978; Di Biase *et al.* 1997; Di Biase and Pandolfi 1999). Its lowest part, the Monte Rivalta Member, is about 250 m thick, and is composed of conglomerates, sandstones, and pelitic sediments (Marroni *et al.* in press). The dominant middle part is formed by the Val Borbera Unit, which shows clasts composed mostly of limestones, and marlstones deriving from the underlying flysch, with a minor contribution of sandstones, ophiolites, radiolarites or other rocks (Gnaccolini 1974; Di Biase *et al.* 1997). The upper part distinguished as the Persi Member, up to 200 m thick, is composed mostly of ophiolitic material and metamorphosed carbonate clasts. Locally, sandstone lens-shaped lithosomes are present within the conglomerate. They are similar to the turbiditic sandstones of the overlying Monastero Formation (up to 1000 m thick), which are interbedded with mudstones (Gelati 1977; Ghibaudo *et al.* 1985; Mutti *et al.* 1995).

The conglomerates are mostly clast supported. They show variable sorting of clasts and poorly visible, discontinuous bedding. The conglomerates have been interpreted as a fan delta (Gnaccolini 1974, 1982; Gelati and Gnaccolini 1978; Mutti *et al.* 1995) deposited from the south and south-west (Gelati and Gnaccolini 1978, 1982), with a minor contribution from the north (Mutti *et al.* 1995). Its development was

conditioned by the epi-sutural position of the Piedmont Basin during the post-collisional phase of development of the Northern Apennines and the Western Alps, and was controlled by tectonics and sea level changes (Gelati and Gnaccolini 1982; Lorenz 1984; Gelati *et al.* 1993, 1998; Mutti *et al.* 1995). Marroni *et al.* (in press) suggested deposition in a Gilbert-type delta in a pull-apart basin, but this idea is questioned and the fan delta model is favoured (Uchman *et al.* 2017a).

The clasts with the etching trace presented occur only in one locality, Montebore (Text-fig. 1; GPS coordinates N44°45.626'; E009°01.079') in the northern termination of the Savignone Conglomerate, at least a few tens of metres above its base. They were found on a slope along a dirt road. The boring-bearing clasts were broken in the field or collected without breaking. The broken surfaces revealed cross-sections of other borings recorded in the locality studied.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Solealites* igen. nov.

DIAGNOSIS: Shallow, oval depression in a lithic substrate with an elevation in the centre.

DERIVATION OF NAME: From Latin *solea* – hoof, in correspondence to the shape of the trace, and *lites*, the common ending for bioerosion ichnogenera.

REMARKS: The described trace fossil (see next section) is somewhat similar to *Sedilichnus* Müller, 1977, which is a shallow depression oval in outline in a Cretaceous sponge from Germany. Irrespective of the fact that it is unclear if *Sedilichnus* is a bioerosion trace, a bioclastration structure or a part of the sponge morphology, and that this name is taxonomically unavailable (Wisshak *et al.* 2015), it shows a flat bottom and no elevation in the centre.

Oichnus excavatus Donovan and Jagt, 2002, transferred to *Tremichnus* Brett, 1985 by Wisshak *et al.* (2015), is a circular pit in a shell with a central, semi-rounded elevation, but it is much smaller (up to 3–4 mm) and the elevation is depressed in respect to the surrounding area; it was produced only in irregular echinoid tests, probably by non-predatory eulimid prosobranch gastropods (Donovan and Jagt 2002), and is even considered as an embedment structure (Donovan and Jagt 2004). Whatever is the taxonomic position of this structure, it is very different from the ichnospecies of *Solealites* described in this paper, which does not fit to *Oichnus* or *Tremichnus*. The latter are small structures in shells or tests (see Wisshak *et al.* 2015). *Loxolenichnus* Breton and Wisshak in Breton *et al.*, 2017, including the former *Oichnus halo*, now *L. halo* (Neumann and Wisshak, 2009), is an oval or circular depression in shelly substrates but with a distinct central hole or a pit; the depression may show concentric grooves. *Ophthalmichnus lyolithon* Wisshak, Alexandrakis and Hoppenrath, 2014 is a microscopic, oval to mostly elliptical attachment scar produced in calcareous substrates by diatoms. It contains a single prominent, median groove. In some cases, it does not show a central elevation and some xenoglyphs of the producers may be observed. The size itself is not the ichnotaxobase (Bertling *et al.* 2006), but large size differences (a few magnitudes in the discussed cases) are a kind of warning that the similarities may be apparent. Poorly preserved *Centrichnus* Bromley and Martinell, 1991 can be mistaken for *Solealites*, but the former has very characteristic internal ornamentation and occurs in skeletal elements. *Annelusichnus circularis* Santos, Mayoral and Muñiz, 2005, produced by balanids, is much shallower and shows concentric structures inside. It does not have any elongated central elevation (Santos *et al.* 2005).

Other bioerosion traces are dissimilar to the described ichnospecies of *Solealites*. However, it shows

some similarities to unnamed, recent etching traces (see Discussion). Therefore, it is distinguished as a new ichnogenus and a new ichnospecies.

Solealites ovalis isp. nov.

(Text-figs 2 and 3)

TYPES AND OTHER MATERIAL: Holotype – specimen illustrated in Text-fig. 2A, B on a pebble (sample 7412), housed in the Crocefieschi Museum (Province Genova) in Liguria, Italy. Other two specimens on the pebble (Text-fig. 2C) are paratypes. Specimen INGUI252P39 (Text-fig. 2E), which is the paratype, and two specimens INGUI252P40 (Text-fig. 3B) and INGUI252P41 (complete specimen in Text-fig. 3A) are housed in the Nature Education Centre (CEP) of the Jagiellonian University – Museum of Geology in Kraków, Poland.

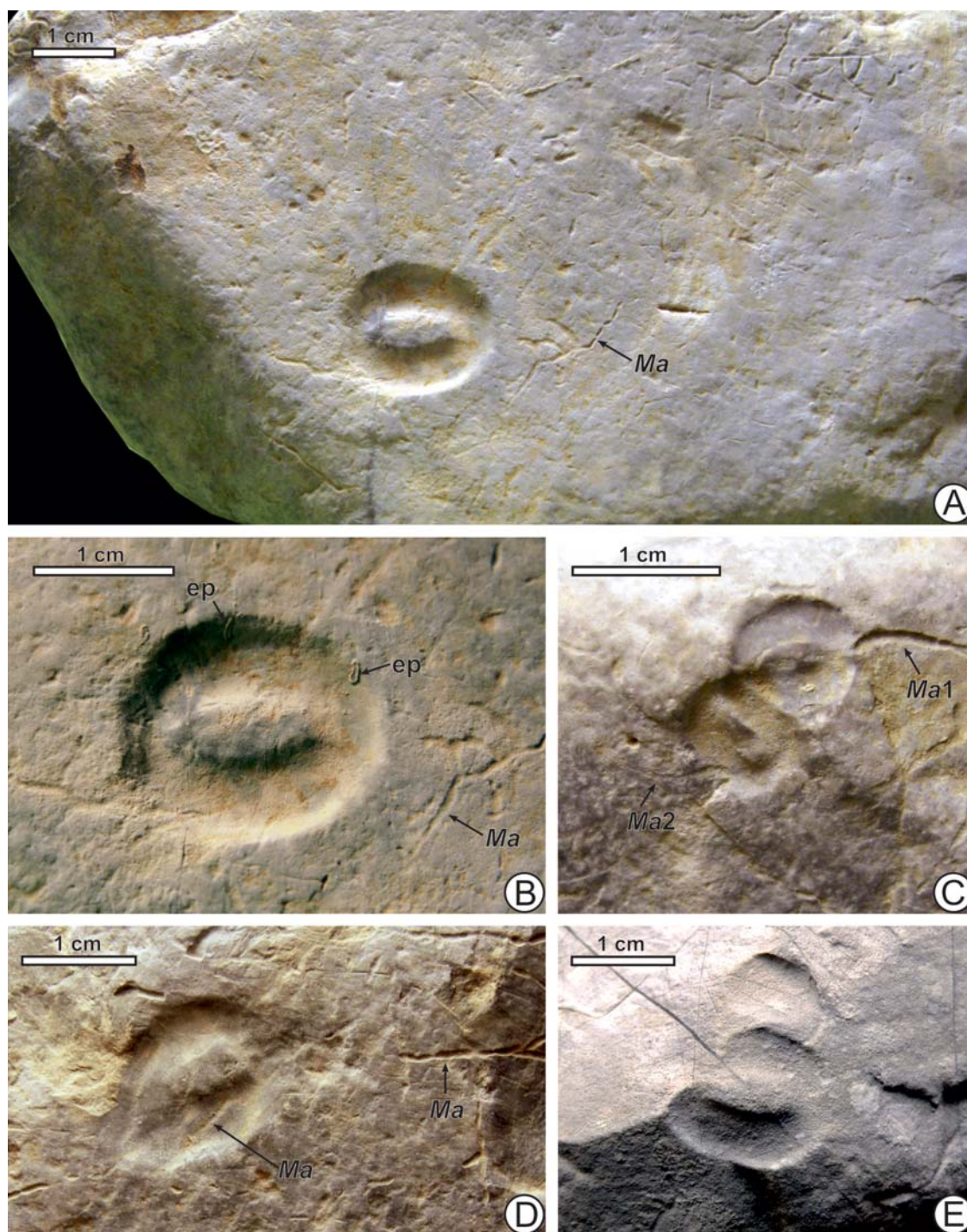
TYPE LOCALITY: Montebore, SW of Grondona, NW Italy.

TYPE HORIZON: Savignone Conglomerate (lower Oligocene: lower–middle Rupelian).

DERIVATION OF NAME: From Latin *oval*, which means also oval in English, in reference to the outline of the trace.

DIAGNOSIS: Shallow, oval depression in lithic substrate with a flat top elevation in the centre. The elevation is elongated according to the main axis of the depression. Its top is on the level of the surrounding area.

DESCRIPTION: Shallow depression, up to 1–2 mm deep, 8.3–18.3 mm long (16.3 mm in the holotype), 7–21 mm wide (14.9 mm in the holotype), with flat elevation in the middle and even margins. Outline oval; in some specimens, including the holotype, regularly elliptical. Elevation shows even margins, rounded terminations and is elongated according to the axis of the depression. Elevation is widest in the middle or one third of its length. Length of elevation 5.1–11.3 mm (9.1 mm in the holotype), width 1.9–7 mm (4.7 mm in the holotype). Flat top of elevation situated on level of the trace surroundings. Therefore, depression forms shallow, flat-bottom moat, whose external margin marks trace outline. Moat maximally 2.2–6.3 mm wide (5.5 mm in the holotype), narrower at one end of the elevation compared to the other end and the sides. Macroscopically and under a binocular

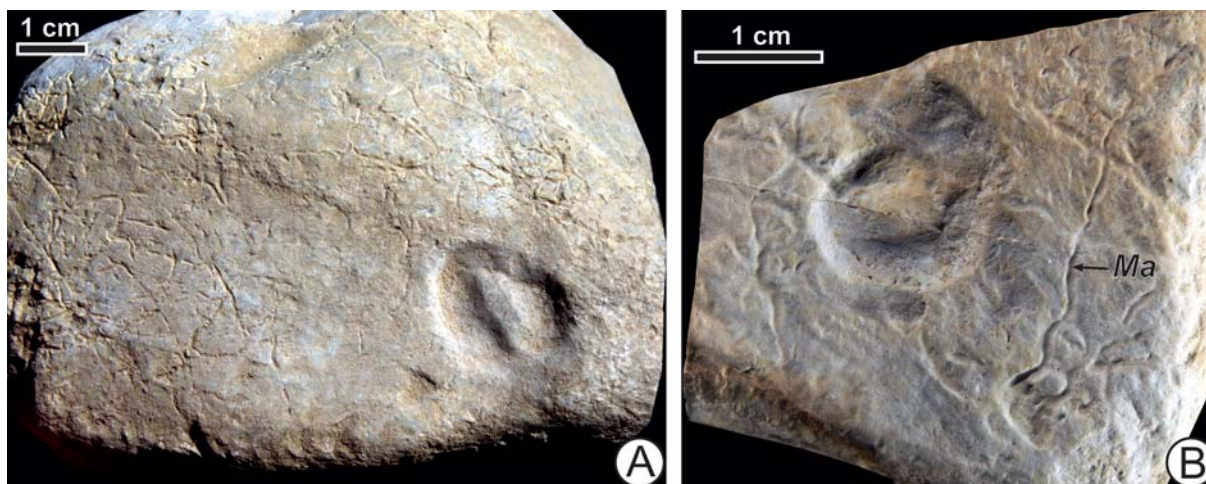


Text-fig. 2. *Solealites ovalis* igen. nov., isp. nov. from the Savignone Conglomerate (Oligocene) at Montebore, NW Italy. *Ma*, *Ma1*, *Ma2* – *Maeandropolydora* cf. *sulcans* Voigt, 1965. A – Holotype in sample 7412. B – Detail of A; ep – epibiont. C, D – Traces in sample 7412, paratypes in C. E – Paratype, INGJ252P39

microscope, no sign of ornamentation inside the trace or its surroundings.

Specimen illustrated in Text-fig. 2D is atypical,

with slightly pear-like outline. Its central elevation slightly oblique in respect to trace main axis and widest from one end. Specimen INGJ252P40 (Text-



Text-fig. 3. *Solealites ovalis* igen. nov., isp. nov. from the Savignone Conglomerate (Oligocene) at Montebore, NW Italy. *Ma* – *Maeandropolydora* cf. *sulcans* Voigt, 1965. A – Field photograph of partly recovered specimen INGUJ252P39 with abundant *Maeandropolydora* cf. *sulcans* Voigt, 1965. B – INGUJ252P39 with an overlap of spiral trace on *S. ovalis*

fig. 3B) shows some overlap of spiral structure, which turns sinistral and prolongs continuously from the moat. The structure terminates outside the trace and becomes wider toward the termination.

Traces preserved on surface of grey marly limestone pebbles deriving from the Upper Cretaceous–Paleocene flysch sediments that underlie the conglomerate. Pebbles are 8–16 cm in size, sub-rounded, crudely blade- or disc-shaped, showing nearly flat surfaces corresponding to the bedding. Some pebbles show branched tunnels or furrows. The holotype, in its external flank of the moat shows an encrusted, elongated, segmented (?), flat structure, which is 1.1 mm long and about 0.5 mm wide.

REMARKS: The pear-like trace (Text-fig. 2D) is ascribed tentatively to *Solealites ovalis* igen. nov., isp. nov., mostly because it is represented by only one specimen. It is unclear if its morphology is within the variability of the ichnospecies or whether it represents a different ichnospecies of *Solealites*. The differences in size can be referred to the ontogenetic development of the trace makers.

ASSOCIATED BORINGS

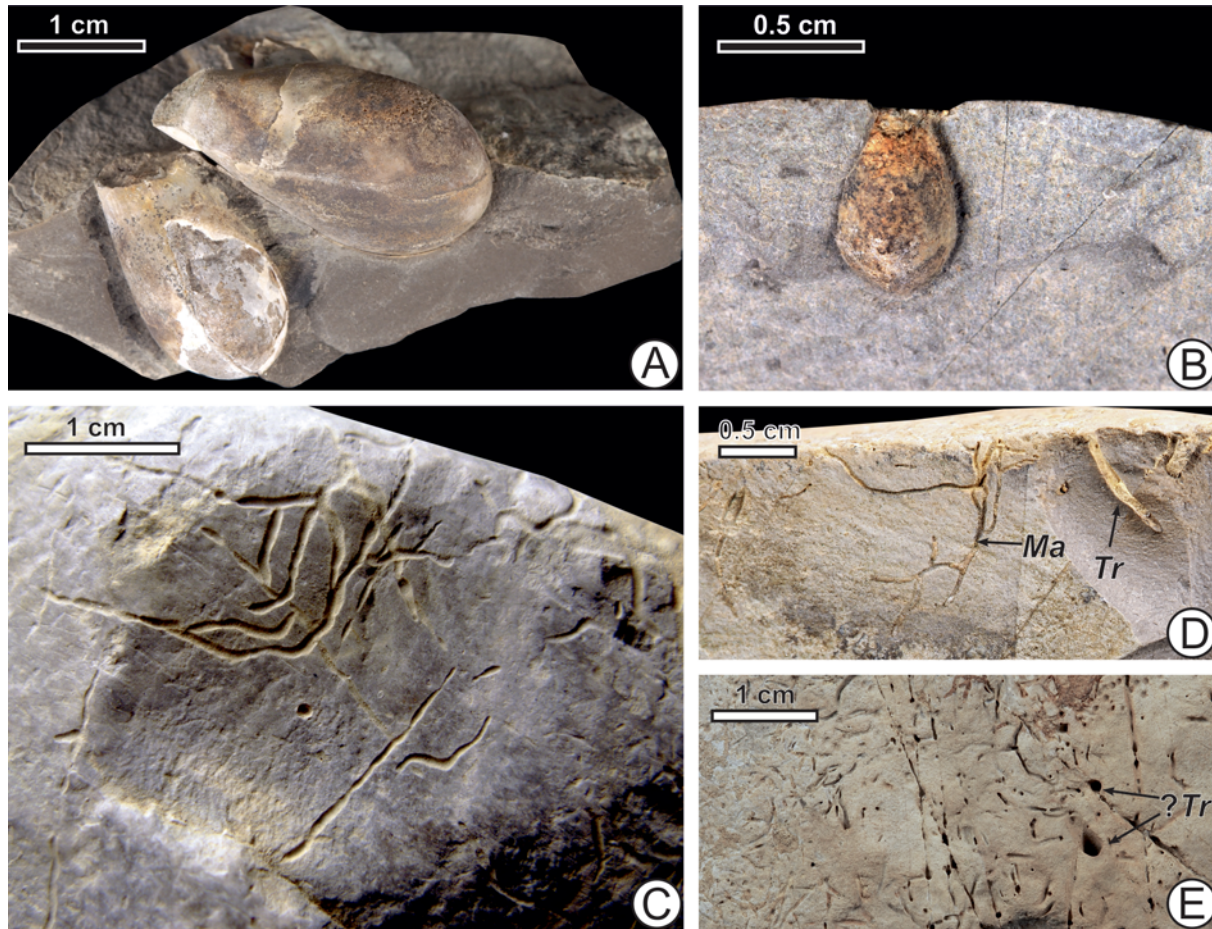
The clasts bearing *Solealites ovalis* igen. nov., isp. nov. usually contain another boring *Maeandropolydora* cf. *sulcans* Voigt, 1965. Other clasts from the locality studied are very occasionally bored. They contain *Maeandropolydora* cf. *sulcans*, ?*Trypanites*

solitarius (Hagenow, 1840) or *Gastrochaenolites lapidicus* Kelly and Bromley, 1984.

Gastrochaenolites lapidicus (Text-fig. 4A, B) occurs in the study site in a few pebbles other than those with *Solealites ovalis* igen. nov., isp. nov. It shows a smooth, ovate chamber filled with sediment and a rounded perpendicular section. It is 21.2–27.7 mm long and maximally 1.4–14.2 mm wide, with the widest part about one third of length from the base. It is partially covered with a thin calcite lining. The neck is very short or it could be broken during collection. A minute specimen (Text-fig. 4B), 6.1 mm long and up to 3.7 mm wide, probably belongs to the same ichnospecies.

Kelly and Bromley (1984) proposed the species of *Lithophaga* Röding, 1798 (Mytilidae) and *Hiatella* Bosc, 1801 (Hiatellidae) as the producers of *Gastrochaenolites lapidicus*. Bromley and Asgaard (1993) included *Gastrochaena dubia* (Pennant, 1777) (Gastrochaenidae), actually *Rocellaria dubia* (see Carter *et al.* 2008), into the producers of *G. lapidicus* but noticed that it also can produce *G. dijugus* Kelly and Bromley, 1984. Uchman *et al.* (2017a) suggested also *Parapholas* sp. (Pholadidae) as potential producers, because its shells occur in *G. lapidicus* from the Savignone Conglomerate.

Maeandropolydora cf. *sulcans* (Text-figs 2A–D, 3A, B, 4C–E) is an irregularly winding, curved or locally straight, branched surface furrow or subsurface, variable oriented, filled or partially unfilled, branched tunnel, 0.3–0.8 mm in diameter. Quite frequently, the furrows transit to tunnels, therefore they



Text-fig. 4. Associated bioerosion trace fossils from the Savignone Conglomerate (Oligocene) at Montebore. **A** – *Gastrochaenolites lapidicus* Kelley and Bromley, 1984, INGUJ252P35. **B** – Minute example of *Gastrochaenolites lapidicus* Kelley and Bromley, 1984, INGUJ252P37. **C** – *Maeandropolydora* cf. *sulcans* Voigt, 1965, INGUJ252P36. **D** – *Maeandropolydora* cf. *sulcans* Voigt, 1965 (*Ma*) and *?Trypanites solitarius* (Hagenow, 1840) (*Tr*), INGUJ252P36. **E** – *Maeandropolydora* cf. *sulcans* Voigt, 1965 and a boring tentatively included in *?Trypanites solitarius* (Hagenow, 1840) (*?Tr*), INGUJ252P36

are the same trace fossil. The tunnels plunge into the pebble up to 15 mm from the surface. This boring co-occurs commonly with *Solealites ovalis* igen. nov., isp. nov. The latter can be cross-cut by *M. cf. sulcans* or vice versa.

Maeandropolydora sulcans shows a very few similarities with other ichnospecies of *Maeandropolydora*, mostly the absence of parallel tunnels (see Bromley and D'Alessandro 1983). A similar boring was described as *M. cf. sulcans* (Cáceres *et al.* 2014) and Uchman *et al.* (2017a), the latter from the Savignone Conglomerate.

?Trypanites solitarius (Text-fig. 4D) is a curved tunnel, 0.8 mm wide, at last 8.5 mm long, oblique in respect to the pebble surface. It is distinctly wider than the adjacent *Maeandropolydora* cf. *sulcans*,

whose tunnels are 0.3–0.4 mm in diameter (Text-fig. 4D). However, only one specimen does not permit a more accurate determination. Even more problematic is the wide, U-shaped, unfilled tunnel, which is 2 mm in diameter, whose outlets are 9 mm apart (Text-fig. 4E). *Trypanites* is a boring of a “worm”, which can belong to polychaetes, sipunculoids and acrothoracican barnacles (Ekdale *et al.* 1984; see also Bromley and D'Alessandro 1987).

DISCUSSION

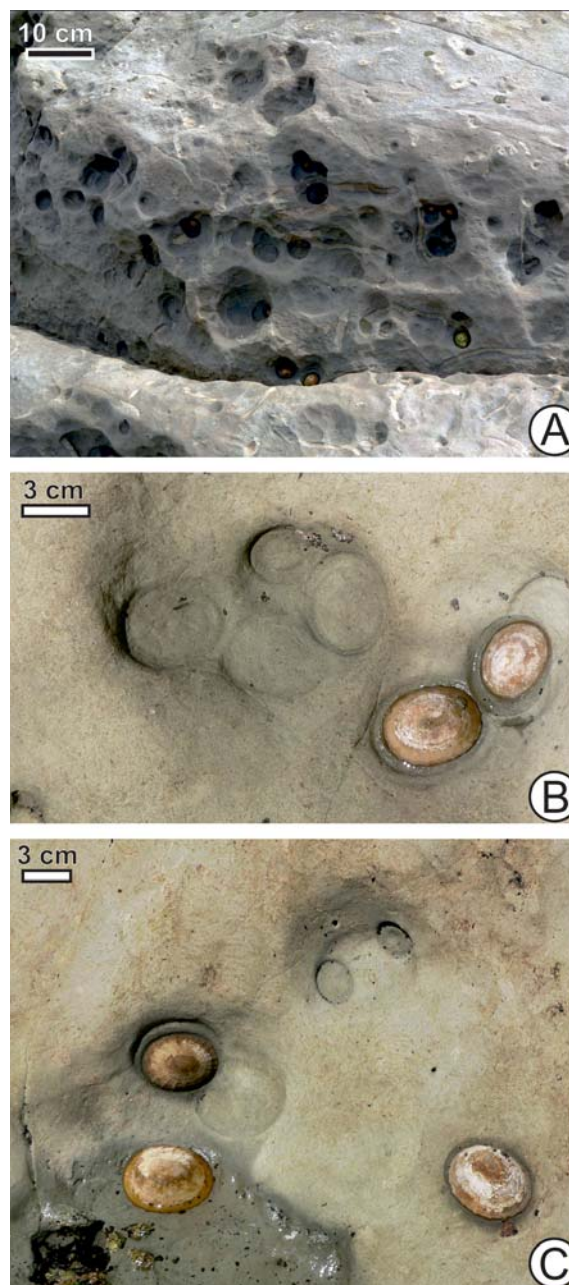
The shallow surface occurrence of *Solealites ovalis* igen. nov., isp. nov. on a lithified substrate allows its classification as an etching trace produced

by an organism attaching itself to the substrate (see Bromley and Heinberg 2006 for a summary on this type of traces). As no body fossils or other direct evidence of the trace maker of these traces can be detected, only an indirect deduction may be offered.

The oval, nearly elliptical shape suggests limpet gastropods, which are common animals attaching themselves to hard substrates, mainly in the intertidal and shallow subtidal rocky shores. Limpet gastropods are a taxonomically diverse group, represented mainly by the clade Patellogastropoda, known also as true limpets. They scrape algae using a radula and come back to the same place called the “home scar” (e.g., Beckett 1968; Lindberg 1975; Warme 1975; Smith 1992). They recognize their own path for coming back to the home scar, within which they are well fitted (e.g., Stephenson 1936; Cook *et al.* 1969; Hirano and Inaba 1980; Faladu *et al.* 2014). The home scar protects the snail against wave action and desiccation (Lord *et al.* 2011; Heller 2015) and reduces predation (Branch 1978, 1981; Garrity and Levings 1983). Some limpets are able to defend their home scars (Heller 2015).

Some of the home scars are bioeroded by the limpets in different substrates, including wood and rocks of different composition and hardness, for instance basalts, and they appear as cavities (Lindberg and Dwyer 1982). Such bioeroded home scars produced by limpets have been mentioned several times in the literature (e.g., Gray 1833; Dall 1870; Hawkshaw 1878; Stephenson 1936; Beckett 1968; Branch 1975; Lindberg 1975; Warme 1975; Smith 1992), but their photographs or drawings are uncommon (but see Abe 1940; Lindberg and Dwyer 1982; Trudgill 1988; Crothers 2003; Bromley and Heinberg 2006; Kázmér and Tabaroši 2012). In the fossil state, a similar scar determined as *?Lacrimichnus* was described from the Upper Cretaceous of the Netherlands (Jagt 2007). Moreover, circular depressions with gentle slopes and a slightly concave downwards bottom in an Upper Cretaceous shell of the ammonite *Pachydiscus* were interpreted as the home scars of limpets (Kase *et al.* 1994). Holes in the shell of the Upper Cretaceous ammonite *Placenticeras* were interpreted as pits produced by limpets rather than mososaur bites (Kase *et al.* 1998; Seilacher 1998).

Some recent home scars illustrated by Bromley and Heinberg (2006) come from the East Cape region in New Zealand. Examples from the same locality, east of Te Araroa, from a big boulder resting on an abrasion platform exposed during low tide are presented in Text-fig. 5. They were produced by *Cellana flava* (Martyn, 1784) (Nacillidae) known from the



Text-fig. 5. Limpet gastropod *Cellana flava* (Martyn, 1784) home scars in boulders on an abrasion platform, east of Te Araroa, East Cape region, New Zealand. A – Home scars in deep cavities. B, C – Home scars and specimens of *C. flava* in some of them

Indo-Pacific oceans. Its home scars have an elliptical shape, diverse size, slightly elevated centre, and may overlap (Text-fig. 5B, C). Some of them are located in the deepest parts of larger depressions (Text-fig. 5A). Other home scars from the literature show also an elliptical outline, and usually a narrow moat along

the perimeter. They appear as an elliptical or circular ring and may be similar to some Pleistocene etching traces referred to balanids (Miller and Brown 1979), which are distinguished as *Annelusichnus circularis* Santos, Mayoral and Muñiz, 2005, but the better preserved representatives of this ichnogenus should contain some concentric structures inside (Santos *et al.* 2005). Dall (1870) mentioned home scars that are deep around the perimeter and almost not bioeroded in the centre. Lindberg (1975), and Lindberg and Dwyer (1982) presented a different morphology of limpet home scars, which show a shallower part close to the perimeter of the shell and a deeper part related to the foot.

Already Gray (1833) supposed that the home scars of limpets are bioeroded by chemical dissolution. Dall (1870) suggested the work of the radula. Hawkshaw (1878) proposed that the home scars were excavated by the radula and the shell edges. Beckett (1968) supposed that home scars are produced by the shell margin and/or the foot. Branch (1981) excluded the bioerosive action of the shell taking in account its low hardness and pointed to mucous glands that contain mucopolysaccharides and carbonic anhydrase in the mantle edge, which can chemically etch and soften calcium carbonate; after softening, calcium carbonate is removed by means of the radula which contains goethite crystals (see also Lindberg and Dwyer 1982). However, in *Solealites ovalis*, no traces of radulation were found. This may be caused by further mechanical abrasion. The bored clasts in the Savignone Conglomerate, commonly with preserved the shells of producers or secondary cryptobionts in *Gastrochaenolites*, were produced in the intertidal zone and redeposited into the deeper environment on the slope of a fan delta. Several pebbles were mechanically abraded as shown by truncation of the bivalve borings (Uchman *et al.* 2017b). Some scars (*Solealites ovalis* igen. nov., isp. nov.) were abandoned long before final deposition. The spiral structure overlapping *S. ovalis* illustrated in Text-fig. 2D is probably an incipient *Spirolites*, a trace produced by vermetid gastropods attaching to hard substrates (Uchman *et al.* 2017a, 2018). Also the presence of epibionts (serpulids?, foraminifers?) in the moat of the holotype (Text-fig. 2A, B) is evidence of long abandonment. Some *S. ovalis* traces truncate *Maeandropolydora cf. sulcans* (Ma1 in Text-fig. 2C), and the opposite situations are also present (Ma2 in Text-fig. 2C, D). The latter case also shows that *S. ovalis* was already not occupied by the trace maker for a long time. It is possible that limpets used their home scars only for a short time, during the stabili-

zation of clasts. Therefore, traces of radulation were easily abraded.

The main problem in the comparison of recent limpet home scars with *Solealites ovalis* igen. nov., isp. nov. is the absence of a wide moat and the central elevation in the latter. In *S. ovalis*, these morphological elements are distinctly narrower than the overall outline of the trace. However, the knowledge of recent home scars in relation to the high variability of limpets in the Cenozoic should be kept in mind. The function of the central elevation in *S. ovalis* is unclear. It could improve the attachment, or could be a dead zone of etching, where the etching substances are not produced. The wide moat could improve retention of water during occupation at low tide.

Also gastropods other than limpets attach strongly to hard substrates, bioerode, and could be potential trace makers of *Solealites ovalis* igen. nov., isp. nov. Abalones (*Haliotis* Linnaeus, 1758), whose taxa have an elliptical foot in outline, can also produce deep scars in soft rocks (Ault and DeMartini 1987). The limpet-like gastropod *Sabia* Gray, 1840 (Hipponicidae) from the Indo-Pacific tropical zone produces oval depressions with an elevation in the middle in shells of gastropods and hermit crabs (Vermeij 1998). Also *Hipponix* DeFrance, 1819 (Hipponicidae) may produce oval attachment scars on skeletal elements (Cernohorsky 1968; Radwański 1977).

Chitons (marine molluscs of the class Polyplacophora, formerly Amphineura) can produce elongate depressions (Warme 1975; Barbosa *et al.* 2008; Kázmér and Tabaroši 2012) and furrows (Donn and Boardman 1988), which show intense radulation. Kázmér and Tabaroši (2012) describe more rounded home scars of chitons with a steep, uneven margin. However, their morphology is poorly documented and there is no information about a central elevation within them. Sea anemones commonly attach to rocks but their attachment scars are unknown. Their invoking is suggested by the trace fossil *Bergaueria* Prantl, 1945, which is interpreted as a circular or oval burrow of a sea anemone in the sediment showing an elevation in the centre (Pemberton *et al.* 1988). However, chitons and sea anemones are much less probable trace makers than gastropods.

CONCLUSIONS

Solealites ovalis is a new ichnogenus and ichnospecies of a bioerosion trace, characterized by an oval, shallow depression with a central elevation. It is interpreted as the home scar of limpet gastro-

pods. However, other gastropod trace makers are not excluded. It occurs on pebbles of the Oligocene Savignone Conglomerate in NW Italy. The pebbles were redeposited from the intertidal zone or shallow subtidal zone to a deeper sea in a fan delta.

Acknowledgements

The research was supported by the Fondazione Luigi, Cesare e Liliana Bertora. Additional support was provided by the Jagiellonian University. Radek Mikuláš (Prague) and Max Wisshak (Wilhelmshaven) provided helpful reviews.

REFERENCES

- Abe, N. 1940. The homing, spawning and other habits of a limpet, *Siphonaria japonica* Donovan. *The Science Reports of the Tohoku Imperial University, Fourth Series*, **15**, 59–95.
- Anonymous. 1969a. Carta Geologica d'Italia alla scala 1:100.000, Foglio 70, Alessandria, II Edizione. Servizio Geologico d'Italia, Roma.
- Anonymous. 1969b. Carta Geologica d'Italia alla scala 1:100.000, Foglio 71, Voghera, II Edizione. Servizio Geologico d'Italia, Roma.
- Anonymous. 1969c. Carta Geologica d'Italia alla scala 1:100.000, Foglio 83, Rapallo, II Edizione. Servizio Geologico d'Italia, Roma.
- Anonymous. 1971. Carta Geologica d'Italia alla scala 1:100.000, Foglio 82, Genova, II Edizione. Servizio Geologico d'Italia, Roma.
- Ault, J.S. and DeMartini, J.D. 1987. Movement and dispersion of red abalone, *Haliotis rufescens*, in northern California. *California Fish and Game*, **73**, 196–213.
- Barbosa, S.S., Byrne, M. and Kelaher, B.P. 2008. Bioerosion caused by foraging of the tropical chiton *Acanthopleura gemmata* at One Tree Reef, southern Great Barrier Reef. *Coral Reefs*, **27**, 635–639.
- Beckett, T.W. 1968. Limpet movements. An investigation into some aspects of limpet movements, especially the homing behaviour. *Tane*, **14**, 43–63.
- Bertling, M., Braddy, S., Bromley, R.G., Demathieu, G.D., Genise, J.F., Mikuláš, R., Nielsen, J.-K., Nielsen, K.S.S., Rindsberg, A.K., Schlirf, M. and Uchman, A. 2006. Names for trace fossils: a uniform approach. *Lethaia*, **39**, 265–286.
- Bosc, L.A.G. 1801. Histoire naturelle des coquilles, contenant leur description, les mœurs des animaux qui les habitent et leurs usages, vol. 3, 1–292. Deterville; Paris.
- Branch, G.M. 1975. Mechanisms reducing intraspecific competition in *Patella* spp.: Migration, differentiation and territorial behaviour. *Journal of Animal Ecology*, **44**, 575–600.
- Branch, G.M. 1978. The responses of South African patellid limpets to invertebrate predators. *Zoologia Africana*, **13**, 221–232.
- Branch, G.M. 1981. The biology of limpets: Physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology – An Annual Review*, **19**, 235–380.
- Breton, G., Wisshak, M., Néraudeau, D. and Morel, N. 2017. Parasitic gastropod bioerosion trace fossil on Cenomanian oysters from Le Mans, France and its ichnologic and taphonomic context. *Acta Palaeontologica Polonica*, **62**, 45–57.
- Brett, C.E. 1985. *Tremichnus*: a new ichnogenus of circular-parabolic pits in fossil echinoderms. *Journal of Paleontology*, **59**, 625–635.
- Bromley, R.G. and Asgaard, U. 1993. Endolithic community replacement on a Pliocene rocky coast. *Ichnos*, **2**, 96–116.
- Bromley, R.G. and D'Alessandro, A. 1983. Bioerosion in the Pleistocene of southern Italy: ichnogenes *Caulostrepsis* and *Maeandropolydora*. *Rivista Italiana di Paleontologia e Stratigrafia*, **89**, 283–309.
- Bromley, R.G. and D'Alessandro, A. 1987. Bioerosion of the Plio-Pleistocene transgression of southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, **93**, 379–422.
- Bromley, R.G. and Heinberg, C. 1974. Attachment strategies of organisms on hard substrates: A palaeontological view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 429–453.
- Bromley, R.G. and Heinberg, C. 2006. Attachment strategies of organisms on hard substrates: A palaeontological view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 429–453.
- Bromley, R.G. and Martinell, J. 1991. *Centrichnus*, new ichnogenus for centrically patterned attachment scars on skeletal substrates. *Bulletin Geological Society of Denmark*, **38**, 243–252.
- Cáceres, L.M., Muñiz, F., Rodríguez-Vidal, J., Vargas, J.M. and Denaire, T. 2014. Marine bioerosion in rocks of the prehistoric tholos of La Pastora (Valencina de la Concepción, Seville, Spain): archaeological and palaeoenvironmental implications. *Journal of Archaeological Science*, **41**, 435–446.
- Carter, J.G., McDowell, T. and Namboodiri, N. 2008. The identity of *Gastrochaena cuneiformis* Spengler, 1783, and the evolution of *Gastrochaena*, *Rocellaria*, and *Lamychaena* (Mollusca, Bivalvia, Gastrochaenoidea). *Journal of Paleontology*, **82**, 102–117.
- Cernohorsky, W.O. 1968. Observations on *Hipponix conicus* (Schumacher, 1817). *The Veliger*, **10**, 275–280.
- Cook, A., Bamford, O.S., Freeman, J.D.B. and Teideman, D.J. 1969. A study of the homing habit of limpet. *Animal Behaviour*, **17**, 330–339.
- Crothers, J.H. 2003. Rocky shore snails as material for projects (with a key for their identification). *Field Studies*, **10**, 601–634.
- Dall, W.H. 1870. Materials toward a monograph of the Gadiniidae. *American Journal of Conchology*, **6**, 8–22.

- Defrance, M. 1819. Mémoire sur nouveau genre de mollusque. *Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts*, **88**, 215–219.
- Di Biase, B., Marroni, M. and Pandolfi, L. 1997. Age of the deformation phases in the Internal Liguride Units: evidences from Lower Oligocene Val Borbera Conglomerates of Tertiary Piedmont Basin (Northern Italy). *Ofioliti*, **22**, 231–238.
- Di Biase, B. and Pandolfi, L. 1999. I Conglomerati della Val Borbera (Bacino Terziario Piemontese) e relative implicazioni per l'esumazione di unità alpine a metamorfismo di alta pressione / bassa temperatura. *Giornale di Geologia*, **61**, 178–181.
- Donn, T.F. and Boardman, M.F. 1988. Bioerosion of rocky carbonate coastlines on Andros Island, Bahamas. *Journal of Coastal Research*, **4**, 381–394.
- Donovan, S.K. and Jagt, J.W.M. 2002. *Oichnus* Bromley borings in the irregular echinoid *Hemipneustes* Agassiz from the type Maastrichtian (Upper Cretaceous, The Netherlands and Belgium). *Ichnos*, **9**, 67–74.
- Donovan, S.K. and Jagt, J.W.M. 2004. Taphonomic and ethologic aspects of the ichnology of the Maastrichtian of the type area (Upper Cretaceous, The Netherlands and Belgium). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **74**, 119–127.
- Ekdale, A.A., Bromley, R.G. and Pemberton, G.S. 1984. Ichnology: the use of trace fossils in sedimentology and stratigraphy. *Society of Economic Geologists and Paleontologists, Short Course*, **15**, 1–317.
- Faladu, J., Vakani, B., Poriya, P. and Kundu, R. 2014. Habitat preference and population ecology of limpets *Cellana karachiensis* (Winckworth) and *Siphonaria siphonaria* (Sowerby) at Veraval Coast of Kathiawar Peninsula, India. *Journal of Ecosystems*, **2014**, Article ID 874013 (6 pp.)
- Garrity, S.D. and Levings, C.S. 1983. Homing to scars as a defence against predators in the pulmonate limpet *Siphonaria gigas* (Gastropoda). *Marine Biology*, **72**, 319–324.
- Gelati, R. 1977. La successione eo-oligocenica di Garbagna (Alessandria) al margine orientale del Bacino Terziario Ligure-Piemontese. *Rivista Italiana di Paleontologia e Stratigrafia*, **83**, 103–136.
- Gelati, R. and Gnaccolini, M. 1978. I conglomerati della Val Borbera, al margine orientale del Bacino Terziario Ligure-Piemontese. *Rivista Italiana di Paleontologia e Stratigrafia*, **84**, 701–728.
- Gelati, R. and Gnaccolini, M. 1982. Evoluzione tettonico-sedimentaria della zona limite tra Alpi ed Appennini tra l'inizio dell'Oligocene ed il Miocene Medio. *Memorie della Società Geologica Italiana*, **24**, 183–191.
- Gelati, R., Gnaccolini, M., Falletti, P. and Catrullo, D. 1993. Stratigrafia sequenziale della successione oligo-miocenica delle Langhe, Bacino Terziario Ligure-Piemontese. *Rivista Italiana di Paleontologia e Stratigrafia*, **98**, 425–452.
- Gelati, R., Gnaccolini, M. and Petrizzo, M.R. 1998. Synsedimentary tectonics and sedimentation in the Tertiary Piedmont Basin, northwestern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, **104**, 193–214.
- Ghibaudo, G., Clari, P. and Perello, M. 1985. Litostratigrafia, sedimentologia ed evoluzione tettonico-sedimentaria dei depositi miocenici del margine sud-orientale del Bacino terziario ligure-piemontese (Valli Borbera, Scrivia e Lemme). *Bollettino della Società Geologica Italiana*, **104**, 349–397.
- Gibert, J.M. de, Domènech, R. and Martinell, J. 2004. An ethological framework for animal bioerosion trace fossils upon mineral substrates with proposal of a new class, fixichnia. *Lethaia*, **37**, 429–437.
- Gnaccolini, M. 1974. Osservazioni sedimentologiche sui conglomerati oligocenici del settore meridionale del Bacino Terziario Ligure-Piemontese. *Rivista Italiana di Paleontologia e Stratigrafia*, **80**, 85–100.
- Gnaccolini, M. 1982. Oligocene fan-delta deposits in Northern Italy: a summary. *Rivista Italiana di Paleontologia e Stratigrafia*, **87**, 627–636.
- Gnaccolini, M. 1988. Osservazioni sui conglomerati oligocenici affioranti nell'area compressa tra Roccaforte Ligure e Grondona (Alessandria). *Rivista Italiana di Paleontologia e Stratigrafia*, **93**, 521–532.
- Gray, J.E. 1833. Some observations on the economy of molluscos animals, and on the structure of their shells. *Philosophical Transactions of the Royal Society, London*, **123**, 771–819.
- Gray, J.E. 1840. Synopsis of the Contents of the British Museum, 42nd ed., 1–370. G. Woodfall; London.
- Hagenow, F. von 1840. Monographie der Rügen'schen Kreideversteinerungen, 2. Radiarien und Annulaten, nebst Nachträge zur I. Abtheilung. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefactenkunde*, **1840**, 631–673.
- Hawkshaw, J.C. 1878. On the action of limpets (*Patella*) in sinking pits and abrading the surface of the chalk at Dover. *Journal of the Linnean Society, Zoology, London*, **14**, 406–411.
- Heller, J. 2015. Sea Snails: A Natural History, 1–354. Springer; Cham-Heidelberg-New York-Dordrecht-London.
- Hirano, Y. and Inaba, A. 1980. *Siphonaria* (pulmonate limpet) survey of Japan 1. Observations on the behavior of *Siphonaria japonica* during breeding season. *Publications of the Seto Marine Biological Laboratory*, **25**, 323–334.
- Ibbeken, H. 1970. Das ligurische Tongriano, eine resedimentierte Molasse des Nordappennin. *Geologisches Jahrbuch, Beihefte*, **93**, 1–139.
- Jagt, J.W.M. 2007. A Late Cretaceous gastropod homing scar (possibly ichnogenus *Lacrimichnus*) from southern Limburg, The Netherlands. *Scripta Geologica*, **134**, 19–25.
- Kase, T., Johnston, P.A., Seilacher, A. and Boyce, J.B. 1998. Alleged mosasaur bite marks on Late Cretaceous ammo-

- nites are limpet (patellogastropod) home scars. *Geology*, **26**, 947–950.
- Kase, T., Shigeta, Y. and Futakami, M. 1994. Limpet home depressions in Cretaceous ammonites. *Lethaia*, **27**, 49–58.
- Kázmér, M. and Tabaroši, D. 2012. Bioerosion on small scale – examples from the tropical or subtropical littoral. *Hantkeniania*, **7**, 37–94.
- Kelly, S.R.A. and Bromley, R.G. 1984. Ichnological nomenclature of clavate borings. *Palaeontology*, **27**, 739–807.
- Lindberg, D.R. 1975. The home depression of the limpet, *Collisella scabra* (Gould, 1846). *Bulletin of the American Malacological Union, Inc.*, (for 1975), 69–70.
- Lindberg, D.R. and Dwyer, K.R. 1982. The topography, formation and role of the home depression of *Collisella scabra* (Gould) (Gastropoda: Acmaeidae). *Veliger*, **25**, 229–234.
- Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*, 1–824. Laurentius Salvius; Holmiae.
- Lord, J.P., Lyczkowski, E.R. and Wilson, W.H. Jr. 2011. Behavior and microhabitat selection of the tortoiseshell limpet *Testudinalia testudinalis* in the northwest Atlantic intertidal zone. *Journal of Experimental Marine Biology and Ecology*, **407**, 234–240.
- Lorenz, C. 1984. Evolution stratigraphique et structural des Alpes Lignes depuis l'Eocene Supérieur. *Memorie della Società Geologica Italiana*, **28**, 211–228.
- Marroni, M. (coord.) in press. Carta Geologica d'Italia alla scala 1:50.000, Foglio 196, Cabella Ligure. Servizio Geologico d'Italia, Roma.
- Marroni, M., Ottria, G., Pandolfi, G., Catanzariti, R., Bormioli, D., Cucchi, A. and Moletta, G. in press. Note Illustrative della Carta Geologica d'Italia alla scala 1:50 000, Foglio 196, Cabella Ligure, 1–178. Servizio Geologico d'Italia; Roma.
- Martyn, T. 1784. *The Universal Conchologist Exhibiting the Figure of Every Known Shell Accurately Drawn and Painted after Nature with a New Systematic Arrangement*. Vol. 1, 1–39. Issued privately by the author; London.
- Miller, W., III and Brown, N.A. 1979. The attachment scars of fossil balanids. *Journal of Paleontology*, **55**, 208–209.
- Müller, A.H. 1977. Zur Ichnologie der subherzynen Oberkreide (Campan). *Zeitschrift für geologische Wissenschaften, Berlin*, **5**, 881–897.
- Mutti, E., Papani, L., di Biase, D., Davoli, G., Mora, S., Segadelli, S. and Tinterri, R. 1995. Il Bacino Terziario Epimesoalpino e le sue implicazioni sui rapporti tra Alpi ed Appennino. *Memoria di Scienze Geologiche*, **47**, 217–244.
- Neumann, C. and Wisshak, M. 2009. Gastropod parasitism on Late Cretaceous to Early Paleocene holasteroid echinoids – Evidence from *Oichnus halo* isp. n. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284**, 115–119.
- Neumann, C., Wisshak, M., Aberhan, M., Girod, P., Rösner, T. and Bromley, R.G. 2015. *Centrichnus eccentricus* revisited: A new view on anomiid bivalve bioerosion. *Acta Palaeontologica Polonica*, **60**, 539–549.
- Pemberton, G.S., Frey, R.W. and Bromley, R.G. 1988. The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils. *Canadian Journal of Earth Sciences*, **25**, 866–892.
- Pennant, T. 1777. *British zoology*, vol. IV. Crustacea. Mollusca. Testacea. i–viii, 1–154. Benj. White; London.
- Prantl, F. 1945. Two new problematic trails from the Ordovician of Bohemia. *Académie Tchèque des Sciences, Bulletin International, Classe des Sciences Mathématiques, Naturelles et de la Médecine*, **46**, 49–59.
- Radwański, A. 1977. Present-day types of trace in the Neogene sequence; their problems of nomenclature and preservation. In: T.P. Crimes and J.H. Harper (Eds), *Trace fossils 2. Geological Journal, Special Issue*, **9**, 227–264.
- Röding, P.F. 1798. *Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturae quae olim collegerat Joa. Fried. Bolten M. D. p. d. Pars secunda continens Conchylia sive Testacea univalvia, bivalvia et multivalvia*, 1–199. Typis Johan Christi; Hamburg.
- Santos, A., Mayoral, E. and Muñiz, F. 2005. Bioerosion scars of acorn barnacles from the southwestern Iberian Peninsula, Upper Neogene. *Rivista Italiana di Paleontologia e Stratigrafia*, **111**, 181–189.
- Seilacher, A. 1998. Mosasaurs, limpets or diagenesis: How *Platyceraster* shells got punctured. *Mitteilungen des Museums für Naturkunde Berlin geowissenschaftliche Reihe 1*, (for 1998), 93–102.
- Smith, A.M. 1992. Alternation between attachment mechanisms by limpets in the field. *Journal of Experimental Marine Biology and Ecology*, **1600**, 205–220.
- Stephenson, T.A. 1936. The marine ecology of the South African coasts, with special reference to the habits of limpets. *Proceedings of the Linnean Society of London*, **148**, 74–79.
- Trudgill, S. 1988. Integrated geomorphological and ecological studies on rocky shores in southern Britain. *Field Studies*, **7**, 239–279.
- Uchman, A., Kleemann, K. and Rattazzi, B. 2017a. Macroborings, their tracemakers and nestlers in clasts of a fan delta: the Savignone Conglomerate (Lower Oligocene), Northern Apennines, Italy. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **283**, 35–51.
- Uchman, A., Stachacz, M. and Salamon, K. 2017b. A new vermetid gastropod boring from the middle Miocene rocky of Poland. In: *Book of Abstracts, 9th International Bioerosion Workshop, Rome, October 23rd–27th, 2017*, pp. 76–77. Istituto Superiore per la Conservazione e il Restauro; Rome.
- Uchman, A., Stachacz, M. and Salamon, K. 2018 [published online]. *Spirolites radwanskii* n. igen., n. isp. — a vermetid gastropod attachment etching trace from the middle Miocene rocky coast of the Paratethys, Poland. *Journal of Paleontology*, doi.org/10.1017/jpa.2017.95.

- Van der Heide, S. 1941. De geologie van het gebied tussen Scrivia en Stafföra, ten N. van de lijn: Isola del Cantone – Monte Giarolo – Santa Margherita di Bobbio. *Leidsche Geologische Mededeelingen*, **12**, 87–170.
- Vermeij, G.J. 1998. *Sabia* on shells: a specialized Pacific-type commensalism in the Caribbean Neogene. *Journal of Paleontology*, **72**, 465–472.
- Voigt, E. 1965. Über parasitische Polychaeten in Kreide-Austern sowie einige andere in Muschelschalen bohrende Würmer. *Paläontologische Zeitschrift*, **39**, 193–211.
- Warne, J.E. 1975. Borings as trace fossils, and the processes of marine bioerosion. In: R.W. Frey (Ed.), *The Study of Trace Fossils. A Synthesis of Principles, Problems and Procedures in Ichnology*, 181–227. Springer; Berlin.
- Wisshak, M., Alexandrakis, E. and Hoppenrath, M. 2014. The diatom attachment scar *Ophthalmichnus lyolithon* igen. et isp. n. *Ichnos*, **21**, 111–118.
- Wisshak, M., Kroh, A., Bertling, M., Knaust, D., Nielsen, J.K., Jagt, J.W.M., Neumann, C. and Nielsen, K.S.S. 2015. In de fence of an iconic ichnogenus – *Oichnus* Bromley, 1981. *Annales Societatis Geologorum Poloniae*, **85**, 445–451.

Manuscript submitted: 2nd February 2018

Revised version accepted: 23rd May 2018